

NEW TAXA OF *OENOTHERA* L. SECT. *OENOTHERA* (ONAGRACEAE)¹

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ABSTRACT

Several new taxa are described in advance of a complete monograph of *Oenothera* sect. *Oenothera* subsect. *Raimannia*. The populations previously assigned by Munz to *O. laciniata* subsp. *pubescens* are here treated as a species in the new subsect. *Nutantigemma*, which is characterized by nodding buds and a distinct geographical range in montane sites from the western United States south to South America. It forms sterile artificial hybrids with members of subsect. *Raimannia* sensu stricto, which has erect buds and which ranges at low elevations from the central and eastern United States through the plains to eastern Colorado and Texas. Two new outcrossing species, *O. breedlovei* and *O. tamrae*, are differentiated from the permanent structural heterozygote *O. pubescens*, for a total of three species assigned to subsect. *Nutantigemma*.

Subsection *Raimannia* is here divided into two series: series *Candela*, established for the species with densely flowered spikes bearing two or more flowers opening per day, inflorescences without lateral branches, acute to rounded petals, and straight floral tubes (*O. rhombipetala*, *O. heterophylla*, *O. clelandii*, *O. bifrons*, and *O. curtissii*); and series *Raimannia* is restricted to plants with loose inflorescences usually interrupted by lateral branches, usually only one flower opening per day, truncate to emarginate petals, and floral tubes curved upward prior to anthesis (*O. grandis*, *O. falfurriae*, *O. mexicana*, *O. laciniata*, *O. drummondii*, and *O. humifusa*). The new species *Oenothera falfurriae* is described for relictual populations in southeastern Texas that are autogamous but form seven bivalents in meiosis I. It has a unique plastome differentiated from its presumed ancestor *O. grandis* and from the morphologically similar and sympatric *O. laciniata*. The new combination *O. drummondii* subsp. *thalassaphila* is made for the populations in Baja California previously treated as *O. thalassaphila*.

Over 20 years of cultivation of nearly 150 strains for experimental hybridizations, cytological examination, study of breeding systems, and extensive study of herbarium materials, has led to revision of the species referred to subg. *Raimannia* (Rose ex Britton & A. Brown) Munz by Munz (1935, 1965). Extensive analysis of crossing relations has resulted in realignment of a group of 75 species into sect. *Oenothera*, which includes the species referred by Munz to his subg. *Oenothera* and subg. *Raimannia* (Stubbe & Raven, 1979). In turn, this large group of basically intercrossable species was further subdivided into five smaller crossing groups that form highly fertile hybrids and usually have compatible plastids. The first of these groups comprises the South American species, which Dietrich (1977) placed into subsect. *Munzia* W. Dietrich (45 species). The second, subsect. *Oenothera* (13 spp.), was outlined by Raven et al. (1979). The third and most primitive group is subsect. *Emersonia* (Munz) W. Dietrich, Raven & W. L. Wagner (four spp.), revised in 1985 by Dietrich et al. The fourth and fifth groups, subsect. *Raimannia* and the new subsect. *Nutantigemma* described in this

paper, will be the subject of an upcoming detailed revision. Prior to publication of the revision, the present paper makes the new subsection and species available for regional floras and concurrent work on *Oenothera*, including DNA restriction mapping and studies of flavonoids, pollen, and seed anatomy.

SUBSECTION *NUTANTIGEMMA*

Populations occurring in montane sites from the western United States south to South America, referred by Munz (1935, 1965) to a variety or subspecies of *Oenothera laciniata* Hill, are morphologically and genetically distinct from *O. laciniata*. This widespread entity is a permanent translocation heterozygote treated by us as *O. pubescens* Willd. ex Spreng.

Two new Mexican species, closely related to *Oenothera pubescens*, one from the cape region of Baja California and one in the southern Sierra Madre Occidental, were detected during the study of herbarium specimens and cultivation of numerous strains in the experimental gardens (Stubbe & Raven, 1979). They are described here as *O. breedlovei* (bivalent-forming) and *O. tam-*

¹ This work has been supported by a series of grants from the National Science Foundation to Peter H. Raven.

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rae (presumably bivalent-forming). *Oenothera tamrae* is known only from the type collection and has not been grown in the experimental garden. All three species are placed into the new subsect. *Nutantigemma*.

Oenothera L. sect. **Oenothera** subsect. **Nutantigemma** W. Dietrich & W. L. Wagner, subsect. nov. TYPE: *O. pubescens* Willd. ex Spreng.

Oenothera sect. *Onagra* sensu Ser. ex DC., Prodr. 4: 46. 1828, pro parte.

Anogra sensu Wootton & Standley, Contr. U.S. Natl. Herb. 16: 150. 1913, pro parte.

Raimannia sensu Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, pro parte; sensu Sprague & Riley, Bull. Misc. Inform. 200. 1921, pro parte.

Oenothera subg. *Raimannia* sensu (Rose ex Britton & A. Brown) Munz, Amer. J. Bot. 22: 645. 1935, pro parte.

Oenothera sect. *Anogra* sensu Tidestrom, Fl. Ariz. & N. Mex. 273. 1941, pro parte.

Oenothera subg. *Raimannia* sect. *Raimannia* sensu (Rose ex Britton & A. Brown) Munz, N. Amer. Fl. II. 5: 105. 1965, pro parte.

Oenothera sect. *Oenothera* subsect. *Raimannia* sensu (Rose ex Britton & A. Brown) W. Dietrich, Ann. Missouri Bot. Gard. 64: 612. 1977 [1978], pro parte.

Herbae annuae vel probaliter biennes, erectae, rosulatae, simplices vel caules principales ramosi ramis arcuatis e rosula adscendentibus. Folia rosulae anguste oblanceolata, profunde partita vel quasi integra, acuta; folia caulina angustissime elliptica vel elliptica, anguste oblanceolata vel oblanceolata vel lanceolata vel anguste oblonga, profunde partita vel quasi integra, acuta, folia strigillosa vel villosa, raro glanduloso-pubescentia. Inflorescentiae simplices vel interruptae ramis lateralibus, apice nutantes, gemmae juvenes erectae, vetiores nutantes, maturae demo erectae, flos unus efflorescet per diem per spicam. Tubi florales 1.5–5 cm longi, plerumque rubri illimiti, strigillosi vel villosi et glanduloso-pubescentes. Sepala flavida, saepe rubra illimita vel rubra fasciata ad margines, interdum rubra maculata; pubescentia tubi floralis similis; apices sepalorum 0.1–1 mm longi. Petala late vel latissime obovata, raro rotunda, apice truncata vel retusa, 0.5–3.5 cm longa, 0.6–4 cm lata, flava, rubescentia vel aurantiaca post anthesin. Styli 2–6.5 cm longi, stigmatibus supra antheras elevato vel antheris circumdato. Capsulae cylindricae, 1.8–4.6 cm longae. Semina ambitu elliptica vel rotundata, brunnea vel atrobrunnea, saepe atromaculata, 0.9–1.6 mm longa, 0.6–1 mm crassa. Planta homozygotica et autocompatibilis vel structuraliter chromosomatice heterozygotica complexa. Numerus gameticus chromosomaticus, $n = 7$.

The principal reason for according these three species (*O. pubescens*-group of Stubbe & Raven, 1979) subsectional status is the sterility of hy-

brids in crosses between subsections *Raimannia* and *Nutantigemma*. They range from western Texas west to Arizona and southeastern California, south to Mexico and Guatemala, and one species extends to the Andes of Colombia, Ecuador, and Peru south to the province of Junín. The nodding flower buds on the species of subsect. *Nutantigemma* clearly differentiate them from those of subsect. *Munzia* and subsect. *Raimannia*. This feature is shared with the white-flowered sect. *Kleinia* Munz, sect. *Anogra* (Spach) Endl., sect. *Ravenia* W. L. Wagner, occasionally with *Oenothera caespitosa* Nutt. subsp. *nava-joensis* W. L. Wagner, Stockhouse & Klein [sect. *Pachylophus* (Spach) Endl.], and with the yellow-flowered sect. *Eremia* W. L. Wagner. In *Oenothera fruticosa* L. [sect. *Kneiffia* (Spach) Endl.], which has yellow flowers, the shoot apices, but not the flower buds, are bent downward; a similar condition occurs in *O. speciosa* Nutt. [sect. *Xylopleurum* (Spach) Endl.]. Nodding buds appear to represent, at least for the most part, plesiomorphy rather than convergence.

Another important argument for considering this group a subsection is that these three species are distributed completely allopatrically from subsect. *Raimannia*. The species of series *Nutantigemma* grow exclusively in montane habitats, from 3,900 m down to approximately 1,500 m, while the species of subsect. *Raimannia* grow only at lower elevations. *Oenothera breedlovei* is self-compatible and bivalent-forming; *O. pubescens* is a permanent translocation heterozygote forming a ring of 14 chromosomes in meiosis I and with 40–70% pollen fertility; *O. tamrae* is probably an outcrossing bivalent-former, based on 90–100% fertile pollen in the type collection.

KEY TO THE SPECIES OF SUBSECT.

NUTANTIGEMMA

- 1a. Stigma elevated above the anthers at anthesis; pollen ca. 90–100% fertile; Laguna Mts., Baja California, Mexico, and Nayarit, Mexico.
 - 2a. Lower leaves deeply parted almost to the midrib; mature buds up to 5 mm in diameter; Laguna Mts., Baja California, Mexico *O. breedlovei*
 - 2b. Lower leaves not parted to the midrib; mature buds 5–7 mm in diameter; Nayarit, Mexico *O. tamrae*
- 1b. Stigma surrounded by the anthers; pollen ca. 40–70% fertile; Arizona, Texas, Mexico (except Baja California), Guatemala, Colombia to Peru *O. pubescens*

Oenothera breedlovei W. Dietrich & W. L. Wagner, sp. nov. TYPE: Mexico. Baja California: granitic slopes surrounding long interior valley, [La Laguna], south of Pico La Aguja, Sierra La Laguna, 6,300–6,700 ft., 22 Oct. 1977, *D. E. Breedlove 43362* (holotype, MO-2695034).

Herbae annuae vel biennes, erectae, rosulatae, 2–3 dm altae. Folia profunde partita vel remote vadoseque dentata. Gemmae vetustiores nutantes. Tubi florales 2.4–4 cm longi. Sepala 1.2–2.2 cm longa, saepe rubromaculata, villosa et glanduloso-pubescentia; apices sepalorum 0.5–1 mm longi. Petala 1.6–3.5 cm longa, flava. Capsulae 1.8–4.6 cm longae, strigillosae. Semina 1.2–1.6 mm longa, 0.6–0.7 mm crassa, saepe maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice structuraliter homozygotica, auto-compatibilis.

Erect annual or probably biennial herbs, forming rosettes; stems 2–3(–5) dm long, simple or with a branched main stem and arcuating lateral branches arising from the rosette, usually flushed with red, densely strigillose, sometimes also scattered villous. Rosette leaves narrowly oblanceolate, 4–12 cm long, 0.5–2 cm wide, pinnately parted to remotely and shallowly dentate, the apex acute, gradually narrowed to the petiole; cauline leaves very narrowly elliptic to lanceolate, 2–5 cm long, 0.5–2 cm wide, usually pinnately parted, the apex acute, the base narrowly cuneate, short-petiolate to sessile; bracts lanceolate to narrowly ovate, 1.5–3 cm long, 0.5–1.5 cm wide, deeply parted to remotely shallowly dentate, the apex acute, the base broadly cuneate to narrowly cuneate; leaves and bracts densely strigillose and sparsely villous. Inflorescence usually with lateral branches, the young buds erect, the older ones nodding, becoming erect just before opening. Flowers usually 1 per spike opening near sunset each day. Floral tube flushed with red, 2.4–4 cm long, ca. 1 mm diam., sparsely to densely strigillose, villous, and glandular puberulent. Mature buds oblong, 3–5 mm diam. at the base. Sepals yellowish, often flushed with red, also red maculate and striped at the margins, scattered to densely villous and scattered to densely glandular puberulent, 1.2–2.2 cm long, the free tips 0.5–1 mm long, erect and appressed in bud, strigillose to villous. Petals yellow, broadly obovate to very broadly obovate, retuse, 1.6–3.5 cm long, 1.6–3.7 cm wide. Filaments 1.1–2 cm long; anthers 4–12 mm long; pollen ca. 90–100% fertile. Ovary 1–2.5 cm long, ca. 1.5 mm diam., densely strigillose; style 4–6.5 cm long, the visible part 1.7–2.5 cm long; stigma elevated

above the anthers at anthesis, the lobes 3–6 mm long. Capsule cylindrical, 1.8–4.6 cm long, 3–3.5 mm diam., densely strigillose. Seeds ellipsoid to broadly ellipsoid, brown to dark brown, often with darker flecks, 1.2–1.6 mm long, 0.6–0.7 mm diam., the surface pitted. Self-compatible but modally outcrossing. Gametic chromosome number, $n = 7$ (7_{II} at meiotic metaphase I).

This new species, known only from Laguna Mts., southern Baja California, Mexico, is named in honor of Dennis E. Breedlove (California Academy of Sciences), who has added greatly to our knowledge of Mexico through his extensive and excellent collections and to whom we are indebted for collecting material of this and many other Mexican *Oenothera* species for cultivation at the Botanical Institute of the University of Düsseldorf and at the Missouri Botanical Garden.

Oenothera tamrae W. Dietrich & W. L. Wagner, sp. nov. TYPE: Mexico. Nayarit: Sierra Madre, near Santa Teresa, territory of Tepic, 8 Aug. 1897, *J. N. Rose 2133* (holotype, US-301038; isotypes, NY, UC).

Herbae annuae vel biennes, erectae, rosulatae, 2–4 dm altae. Folia partita seu remote obtuseque dentata vel quasi integra. Gemmae vetustiores nutantes. Tubi florales 3.5–4.2 cm longi, villosi et glanduloso-pubescentes. Sepala 1.8–2.5 cm longa, rubro complana et rubro-fasciata ad margines; apices sepalorum 0.5 mm longi. Petala 2–3.5 cm longa, flava. Capsulae 4–4.5 cm longae, strigillosae et villosae. Semina 1–1.1 mm longa, 0.7 mm crassa.

Erect annual or biennial herbs, probably forming rosettes; stems 2–4 dm long, simple or with obliquely ascending lateral branches arising from the rosette, densely strigillose and sparsely to densely villous. Cauline leaves narrowly elliptic or narrowly lanceolate to lanceolate, 4–8 cm long, 0.8–1.8 cm wide, pinnately parted or remotely and bluntly dentate to subentire, the apex acute, the base narrowly cuneate, sessile; bracts narrowly lanceolate to lanceolate, 3–4.5 cm long, 0.7–1.5 cm wide, remotely and bluntly dentate, the apex acute, the base narrowly cuneate, sessile; leaves and bracts strigillose. Inflorescence simple or with lateral branches, nodding. Usually 1 flower per spike opening probably near sunset each day. Floral tube flushed with red, 3.5–4.2 cm long, 1.5–2 mm diam., sparsely villous and sparsely glandular puberulent. Mature buds cylindrical to narrowly ovoid, 5–7 mm diam. at the base, nodding before anthesis. Sepals yellow-

ish, often flushed with red and striped red at the margins, the pubescence as on floral tube, 1.8–2.5 cm long, the sepal tips ca. 0.5 mm long, erect in bud, strigillose. Petals yellow, very broadly obovate, retuse, 2–3.5 cm long, 3–4 cm wide. Filaments 1.5–1.7 cm long; anthers 6–9 mm long; pollen ca. 90–100% fertile. Ovary 1.8–2.6 cm long, ca. 2 mm diam., densely strigillose and densely villous, the apex also glandular puberulent. Style 5.3–6.4 cm long, the visible part 1.8–2.2 cm long; stigma elevated above the anthers at anthesis, the lobes 5–8 mm long. Capsule cylindrical, 4–4.5 cm long, 3–4 mm diam., the pubescence as on ovary but less dense. Seeds broadly ellipsoid, brown with dark red flecks, 1–1.1 mm long, ca. 0.7 mm diam., pitted. Chromosome number unknown.

This rare new species, known only from the type locality, near Santa Teresa in the Sierra Madra, Nayarit, Mexico, is named in honor of Tamra Engelhorn Raven, botanist and wife of Peter H. Raven. The description is based entirely on the type collection made by J. N. Rose in 1897.

SUBSECTION *RAIMANNIA*

The yellow-flowered species assigned by Munz (1935, 1965) to his subg. *Raimannia* from the central and eastern United States are now considered to comprise subsect. *Raimannia*. Stubbe and Raven (1979), when considering the realignment of sect. *Oenothera*, included *O. grandis* (Britton) Smyth, *O. laciniata* Hill, *O. drummondii* Hook., *O. humifusa* Nutt., *O. heterophylla* Spach, and *O. rhombipetala* Nutt. ex Torrey & A. Gray in subsect. *Raimannia*. Work toward the overall revision of the subsection has led to the recognition of two series within it.

Oenothera* sect. *Oenothera* subsect. *Raimannia
(Rose ex Britton & A. Brown) W. Dietrich
series ***Candela*** W. Dietrich & W. L. Wagner,
series nov. TYPE: *O. rhombipetala* Nutt. ex
Torrey & A. Gray.

Oenothera sect. III Spach, Nouv. Ann. Mus. Hist. Nat. 4: 347. 1835, pro parte.

Oenothera § *Euoenothera* sensu S. Watson, Proc. Amer. Acad. Arts 8: 574. 1873, pro parte.

Oenothera sensu Small, Bull. Torrey Bot. Club 23: 172. 1896, pro parte.

Raimannia sensu Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, pro parte.

Oenothera subg. *Raimannia* sensu Munz, Amer. J. Bot.

22: 645. 1935, pro parte; sensu Sprague & Riley, Bull. Misc. Inform. 200. 1921, pro parte.

Oenothera subg. *Raimannia* sect. *Raimannia* sensu Munz, N. Amer. Fl. II. 5: 105. 1965, pro parte.

Herbae annuae vel biennes, probaliter breviter perennes, erectae, rosulatae, simplices vel caules principales ramosi ramis oblique e rosula adscendentibus, 2.5–10 dm altae. Inflorescentiae densae vel laxae, simplices, non interruptae ramis lateralibus; efflorescunt flores 2 vel complures per diem per spicam. Tubi florales 1.5–4.7 cm longi. Capsulae versus apicem ± angustatae, 1–3.3 cm longae, 2–4 mm crassae. Semina anguste elliptica vel late elliptica, 1.1–1.9 mm longa, 0.4–0.8 mm crassa, plerumque atromaculata.

Series *Candela* comprises a clearly defined group of five closely related species that occur in sandy soil in open places such as fields, prairies, roadsides, and open woods, from southern South Dakota, Minnesota, and Michigan south to Texas and southeastern New Mexico and east to Louisiana, Alabama, northern Florida, and southern Georgia. They all have the presumably derived characters of relatively densely flowered spikes on which two or more flowers open every evening, unlike the species of series *Raimannia*, which nearly always produce only one flower per branch each day, a plesiomorphic characteristic. The spikes of series *Candela* never have lateral shoots, as is often the case in series *Raimannia*. The fully grown buds of series *Candela* are narrowly oblong, whereas those of series *Raimannia* are lanceoloid in the large-flowered structural homozygote species and oblong to ellipsoid in the small-flowered heterozygote species. In series *Raimannia*, the older buds are curved upward until very shortly before flowering; those of series *Candela* are straight. The shapes of the petals also clearly differentiate series *Candela* from series *Raimannia*; those of series *Candela* are acute to rounded at the apex, in contrast with those of series *Raimannia* which are truncate to emarginate. Further, the capsules of series *Candela* are relatively short and thicker toward the base, while those of series *Raimannia* are on average longer and nearly cylindrical. All species of series *Candela* appear to be biennials. In contrast to this specialized habit, the species of series *Raimannia* have evolved an annual habit except *O. drummondii* and *O. humifusa*, which inhabit sand dunes and have retained the generalized perennial habit.

Three of the species, *Oenothera heterophylla*, *O. bifrons* D. Don, and *O. rhombipetala*, are self-incompatible bivalent-formers, and *O. clelandii* W. Dietrich, Raven & W. L. Wagner and *O.*

curtissii (Rose) Small are complex structural heterozygote species, presumably derived from an ancestor similar to *O. rhombipetala*.

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich series **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich & W. L. Wagner, comb. & stat. nov. Based on *Raimannia* Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, ex Britton & A. Brown, Ill. Fl. N. U.S., 2nd edition, 2: 596. 1913. *Oenothera* subg. *Raimannia* (Rose ex Britton & A. Brown) Munz, Amer. J. Bot. 22: 645. 1935. *Oenothera* subg. *Raimannia* sect. *Raimannia* (Rose ex Britton & A. Brown) Munz, N. Amer. Fl. II. 5: 105. 1965. *Oenothera* sect. *Oenothera* subsect. *Raimannia* (Rose ex Britton & A. Brown) W. Dietrich, Ann. Missouri Bot. Gard. 64: 612. 1977 [1978]. TYPE: *O. laciniata* Hill.

Onagra sensu Moench, Methodus 1: 675. 1774, pro parte.

Oenothera sect. *Onagra* sensu Ser. ex DC., Prodr. 4: 46. 1828, pro parte.

Oenothera sect. *Allochroa* sensu Fischer & Meyer, Index Sem. Hort. Petrop. 2: 44. 1835, pro parte.

Oenothera sect. I Spach, Hist. Nat. Vég. 4: 353. 1835, pro parte.

Oenothera sect. III & IV sensu Spach, Nouv. Ann. Mus. Hist. Nat. 4: 347. 1835, pro parte.

Oenothera § *Euoenothera* sensu S. Watson, Proc. Amer. Acad. Arts 8: 574. 1873, pro parte.

Oenothera sensu Raimann, Nat. Pflanzenfam. III. 7: 214. 1893, pro parte; sensu Small, Bull. Torrey Bot. Club 23: 172. 1896, pro parte.

Oenothera sect. *Oenothera* sensu Tidestrom, Fl. Ariz. & N. Mex. 272. 1941, pro parte.

Erect to procumbent, annual or perennial herbs \pm forming rosettes; stems green or flushed with red, simple or much-branched, strigillose or strigillose and villous, sometimes also glandular puberulent especially in the region of the inflorescence. Rosette leaves very narrowly oblanceolate to oblanceolate or lanceolate, parted to dentate, acute; cauline leaves narrowly oblanceolate to oblanceolate, narrowly elliptic, elliptic, narrowly obovate or narrowly oblong, parted to subentire, the lobes \pm dentate, the apex acute, the base narrowly cuneate to acute to almost sessile; all leaves strigillose or strigillose and villous, sometimes also glandular puberulent. Inflorescence lax, often with lateral branches, usually only 1 flower per spike opening near sunset each day. Floral tube 1.5–5 cm long, yellowish, often

flushed with red, rarely also red-flecked, strigillose or glandular puberulent, or villous and glandular puberulent, usually curved upward. Sepals greenish to yellowish, often flushed with red or red-striped at the margins, sometimes red-flecked, the pubescence usually as on floral tube, the sepal tips 0.3–5 mm long, erect and appressed or spreading in bud, sometimes separated. Petals very broadly obovate, truncate to emarginate at apex, 0.5–4.5 cm long, 0.5–5.5 cm wide, yellow, sometimes pale yellow, fading red to orange after anthesis. Style 2–7.5 cm long; stigma elevated above the anthers at anthesis or surrounded by the anthers and pollen shed directly onto it. Capsule cylindrical, 2–5.5 cm long, 2–5 mm diam. Seeds ellipsoid to subglobose, brown, sometimes with darker flecks (*O. drummondii*, *O. humifusa*), 0.8–2 mm long, 0.3–0.9 mm diam. Self-incompatible (1 sp.) or self-compatible and modally outcrossing (1 sp.) to modally autogamous (2 spp.), or permanent structural heterozygotes (2 spp.). Gametic chromosome number, $n = 7$ (7_{II} , $\odot 14$ or intermediate chromosome configurations at meiotic metaphase I).

Series *Raimannia* of subsect. *Raimannia* is comprised of six species occurring in open, sandy, and disturbed places, sometimes on dunes, from North Dakota south to Texas and east to the Atlantic Coast, in Mexico along the Gulf Coast, and disjunct in southern Baja California. The species exhibit considerable variation; among them, however, only *Oenothera drummondii* can be subdivided into two geographically separated subspecies. Typical of the species of series *Raimannia* are loose inflorescences, which often have lateral branches, and upward-curving flower buds. Comparisons with series *Candela* were made in the discussion of that series.

The distribution of series *Raimannia* is essentially the same as that of series *Candela* but extends farther east, to the Atlantic Coast, and extends south to the state of Campeche, Mexico, along the coast of the Gulf of Mexico. *Oenothera drummondii* Hook. subsp. *thalassaphila* (Brandegee), comb. nov. is disjunct, occurring along the Pacific Coast at the southern tip of Baja California, Mexico.

Oenothera grandis (Britton) Smyth, *O. falfuriae* (described as new below), *O. mexicana* Spach, and *O. drummondii* form bivalents, whereas *O. laciniata* Hill and *O. humifusa* Nutt. are permanent structural heterozygotes. In this section only *O. grandis* is self-incompatible; all

other species, both bivalent-formers and complex structural heterozygotes, are self-compatible and largely autogamous.

Oenothera falfurriae W. Dietrich & W. L. Wagner, sp. nov. TYPE: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 2 July 1981, cult. no. 81-115 from seeds collected in U.S.A. Texas: Brooks Co., 13.3 mi. S of junction of Highways 281 and 285 in Falfurrias, 10 May 1978, K. Allred & R. Shaw 2021 (holotype, MO-3332203; isotypes, DUSS, M, MO).

Herbae annuae, erectae vel parum decumbentes, rosulae foliis paucis, 1–4 dm altae. Folia partita vel breviter dentata vel quasi integra. Gemmae erectae. Tubi florales 2.5–4 cm longi, villosi et glanduloso-pubescentes. Sepala 1–2.2 cm longa, viridi-flava, immaculata vel rubromaculata; apices sepalorum minuti, 0.5–2 mm longi. Petala 1.3–2.5 cm longa, flava vel pallide flava. Capsulae 2–4.5 cm longae, 2–2.5 mm crassae, strigillosae, villosae et glanduloso-pubescentes. Semina 0.8–1.4 mm longa, 0.3–0.6 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice structuraliter homozygotica, autocompatibilis.

Erect to decumbent annual herbs, forming a rosette with only a few leaves; stems 1–4 dm long, usually simple, densely to sparsely strigillose, villous and sometimes also glandular puberulent. Rosette leaves oblanceolate, 5–12 cm long, 1.3–3.5 cm wide, dentate to pinnatifid or sometimes subentire, the apex acute, gradually narrowed to a short petiole; cauline leaves narrowly oblanceolate to elliptic or narrowly lanceolate, 2–8.5 cm long, 1–3 cm wide, usually dentate, occasionally pinnatifid or subentire, the apex acute, gradually narrowed to subsessile base; bracts elliptic, narrowly ovate to lanceolate, 2–4.5 cm long, 0.5–2.5 cm wide, dentate or subentire to pinnately lobed, narrowed to the base, subsessile; all leaves densely to sparsely villous and glandular puberulent, especially on the midrib of the lower surface and along the margin, usually also sparsely to moderately strigillose. Inflorescence lax, simple or with lateral branches, usually only 1 flower per spike opening near sunset each day, erect at anthesis. Floral tube 2.5–4 cm long, densely to sparsely villous and glandular puberulent. Mature buds lanceoloid to narrowly ovoid or oblong-ovoid, 0.4–0.6 cm diam.

at the base. Sepals green to greenish yellow, sometimes with red spots, the pubescence as on the floral tube, 1–2.2 cm long, the sepal tips 0.5–2 mm long, erect in bud, strigillose and villous. Petals yellow, broadly obovate, 1.3–2.5 cm long, 1.4–2.7 cm wide, the apex truncate to slightly retuse. Filaments 10–17 mm long; anthers 4–5 mm long; pollen ca. 90–100% fertile. Ovary 1–1.7 cm long, ca. 1.5 mm diam., densely villous, strigillose and glandular puberulent; style 3.5–5 cm long, the visible part 1.2–3 cm long; stigma usually elevated above the anthers at anthesis, the lobes 3–7 mm long. Capsule cylindrical, 2–4.5 cm long, 2–2.5 mm diam., the surface pitted. Seeds brown, ellipsoid, 0.8–1.4 mm long, 0.3–0.6 mm diam. Self-compatible, modally autogamous. Gametic chromosome number, $n = 7$ (7_{II} at meiotic metaphase I).

Oenothera falfurriae, named after Falfurrias, Brooks County, Texas, where the type was collected, is endemic to open sandy sites in southeastern Texas. Its range is nearly the same as those of *O. bifrons* and *O. mexicana*. When Dietrich first detected the species, the specimens were treated as hybrids between *O. grandis* and *O. laciniata* since they were somewhat intermediate between these species. Seed samples collected by K. Allred and R. Shaw made it possible to cultivate this species at the Botanical Institute in Düsseldorf, and it soon became obvious that the plants were by no means hybrids, but instead represented an undescribed bivalent-forming species. All plants examined formed 7_{II} in meiosis, and no individuals grown from seed resembled either *O. laciniata* or *O. grandis*. The individual collection numbers of Allred and Shaw represent population samples of several plants from which seeds were taken and sowed separately: 2016, 2020, and 2021 contained *O. falfurriae* and *O. laciniata*; 2018 contained *O. falfurriae* and *O. mexicana*. Seeds taken from plants of *O. falfurriae* produced only *O. falfurriae* and those of *O. laciniata* produced only *O. laciniata*.

Oenothera falfurriae differs from *O. grandis* in its self-compatibility and smaller petals, which are intermediate in size between those of *O. laciniata* and those of *O. grandis*. Stigmas in the closed mature buds are only slightly raised above the anthers, suggesting that self-pollination is common in *O. falfurriae*. Also, the shape of the buds is more or less oblong, in contrast with the lanceoloid buds of *O. grandis*, and the sepals in *O. falfurriae* are very delicate and pressed to-

gether in bud, whereas in *O. grandis* they are often spreading, longer, and thicker.

Oenothera falfurriae is narrowly distributed and presumably relictual. It appears to maintain itself distinct from the other species of series *Raimannia* with which it grows sympatrically—*O. grandis*, *O. laciniata*, and *O. mexicana*—by possessing a unique plastome. Artificial crosses made by Dr. Behn at the Botanical Institute in Düsseldorf showed that crosses between *O. drummondii* or *O. humifusa* and *O. falfurriae* as the staminate parent produced pale seedlings that failed to grow beyond the cotyledon stage. Similarly, the seeds of crosses between *O. grandis* and *O. falfurriae* did not germinate at all (Behn, pers. comm.). Also, since crosses between *O. drummondii*, *O. humifusa*, or *O. grandis* and *O. laciniata* produce completely green and viable offspring, we can assume that similar crossing barriers exist between *O. falfurriae* and *O. laciniata*, based on the pattern of such relationship in *Oenothera* sect. *Oenothera* generally.

***Oenothera drummondii* Hook. subsp. *thalassaphila* (Brandege) W. Dietrich & W. L. Wagner, comb. nov.** Based on *Oenothera thalassaphila* Brandege, Univ. Calif. Publ. Bot. 10: 185. 1922. *Oenothera drummondii* Hook. var. *thalassaphila* (Brandege) Munz, Amer. J. Bot. 22: 651. 1935. TYPE: Mexico. Baja California Sur: San José del Cabo, 12 Mar. 1892, T. S. Brandege 218 (lectotype, UC-107674; see Munz, Amer. J. Bot. 22: 651. 1935).

The separation of *Oenothera drummondii* subsp. *thalassaphila*, which is restricted to dunes of coastal southern Baja California del Sur, Mexico, from subsp. *drummondii* depends on a combination of characters since no single morphological feature separates them clearly. *Oenothera drummondii* subsp. *thalassaphila* always grows

for several years, as is demonstrated by the consistent presence of nonflowering shoots and large taproots on the older plants. By contrast, *O. drummondii* subsp. *drummondii* is basically an annual, seldom overwintering for a second season; it usually has only a few nonflowering shoots or none, and the development of its taproot is considerably weaker than in subsp. *thalassaphila*. In general, the habit of subsp. *drummondii* is more upright than that of subsp. *thalassaphila*, which has prostrate to ascending stems. In addition, the calyx of subsp. *thalassaphila* often has red spots and lacks glandular hairs, whereas the calyx of subsp. *drummondii* only rarely has reddish spots and is often glandular puberulent. The sizes of the capsules and seeds are also modally distinct: in subsp. *thalassaphila* the capsules are 2–4 cm long and 2.5–5 mm in diameter, and the seeds are 1.5–2 mm long and 0.7–0.9 mm in diameter; in subsp. *drummondii* the capsules are 2.5–5.5 cm long and 2–3 mm in diameter, and the seeds are 1.1–1.7 mm long and 0.5–0.8 mm in diameter.

LITERATURE CITED

- DIETRICH, W. 1977 [1978]. The South American species of *Oenothera* sect. *Oenothera* (*Raimannia*, *Renneria*; Onagraceae). Ann. Missouri Bot. Gard. 64: 425–626.
- , P. H. RAVEN & W. L. WAGNER. 1985. Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae). Syst. Bot. 10: 29–48.
- MUNZ, P. A. 1935. Studies in Onagraceae. IX. The subgenus *Raimannia*. Amer. J. Bot. 22: 645–663.
- . 1965. Onagraceae. N. Amer. Fl. II. 5: 1–278.
- RAVEN, P. H., W. DIETRICH & W. STUBBE. 1979 [1980]. An outline of the systematics of *Oenothera* subsect. *Euoenothera* (Onagraceae). Syst. Bot. 4: 242–252.
- STUBBE, W. & P. H. RAVEN. 1979. A genetic contribution to the taxonomy of *Oenothera* sect. *Oenothera* (including subsections *Euoenothera*, *Emersonia*, *Raimannia* and *Munzia*). Pl. Syst. Evol. 133: 39–59.